

Upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, Myanmar

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Abstract. Discovery of upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, central Myanmar (= Burma) throws a new light on previously confused species- and genus-level systematics of *Deperetella* and its related genus *Diplophodon*. Clarification of the relationship among the *Deperetella* species is particularly important for correlation of Eocene mammal faunas in Asia. The newly discovered material show the characteristics of the previously unknown upper premolar dentition of *D. birmanica*, demonstrating that *Deperetella similis* (the type species of the genus *Diplophodon*) from China is a junior synonym of *Deperetella birmanica* and that *D. birmanica* is clearly distinguishable from all other species of *Deperetella*. The genus *Diplophodon*, to which *D. birmanica* has often been allocated, is regarded conventionally as a junior synonym of *Deperetella* because this genus is not sufficiently distinct from *Deperetella* to warrant generic separation. The presence of *D. birmanica* and its comparable species in several Eocene deposits of Myanmar, China and Mongolia suggests that these deposits are roughly contemporaneous.

Key words: *Deperetella*, Deperetellidae, *Diplophodon*, Eocene, Myanmar, Pondaung Formation

Introduction

Deperetella is an Asian Eocene tapiroid perissodactyl genus and was proposed by Matthew and Granger (1925a) based on *Deperetella cristata* Matthew and Granger, 1925a as the type species. This genus and *Teleolophus* Matthew and Granger, 1925b, which together constitute the family Deperetellidae Radinsky, 1965, are among the most common elements of the middle to late Eocene mammal fauna in Asia and important for correlation of Eocene mammal faunas in this area. Zdansky (1930) proposed *Diplophodon* and described *Diplophodon similis* as the type species. Of several species in the genus *Deperetella*, *Deperetella birmanica* (Pilgrim, 1925) from the Pondaung Formation, Myanmar has been sometimes referred to the genus

Diplophodon based on their small dental size and several of their dental characteristics (e.g. Ding *et al.*, 1977).

Previous classification of *Deperetella birmanica* and its related species has been much confused because these species were described on the basis of different parts of dentitions. *D. birmanica* was originally described by Pilgrim (1925) as *Chasmodon? birmanicum* based on two mandibular rami of a single individual from the Eocene Pondaung Formation, central Myanmar. This was the only species of the Deperetellidae from the Pondaung Formation, and was questionably referred to the genus *Deperetella* by Colbert (1938). On the other hand, *Diplophodon similis* was described based on an upper dentition from the Heti Formation in the Yuanchu Basin of the Shanxi and Henan Provinces, China (Zdansky, 1930). Young (1937) reported

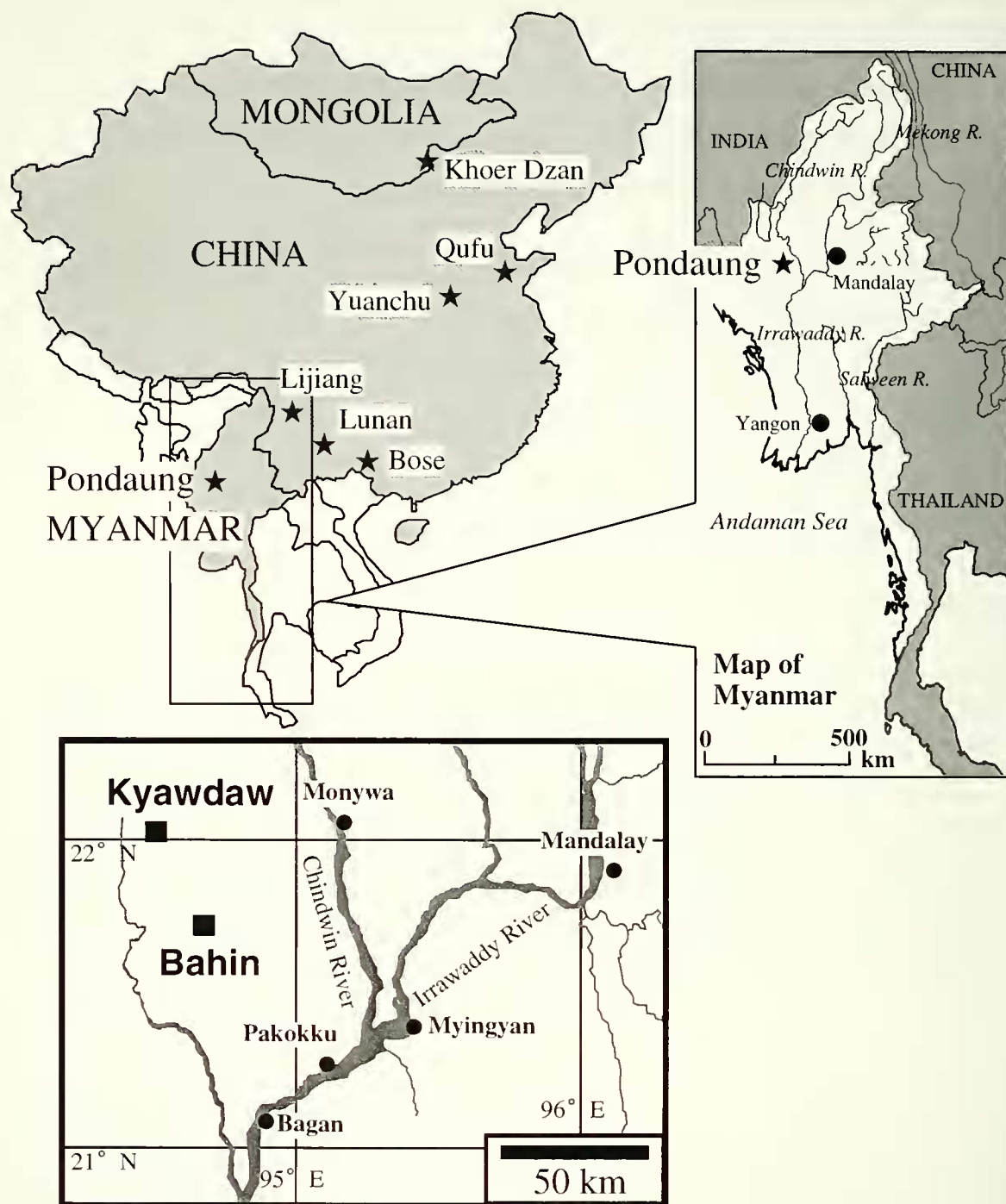


Figure 1. Maps showing distribution of several deperetellid-bearing deposits in Asia, names of place mentioned in this paper, and collecting sites of NMMP-KU 0005 and 0006. **Upper left map** showing locations of deposits that yielded *Deperetella birmanica* (Pilgrim, 1925) or *Deperetella* sp. cf. *D. birmanica* (black stars). Data from Colbert (1938), Li and Ting (1983), Russell and Zhai (1987), Shi (1989), Dashzeveg and Hooker (1997), and Huang (1999). **Upper right map** is topographic map of Pondaung area in central Myanmar, showing some major cities (black circles). **Lower map** showing collecting sites (black squares) of NMMP-KU 0005 and 0006 in the Pondaung Formation.

an additional upper dentition of *D. similis* from the same formation. Radinsky (1965) referred both *Chasmothereium?* *birmanicum* and *Diplophodon similis* to the genus *Deperetella*, and established a new family Deperetellidae. He mentioned that *D. birmanica* was related to *D. similis*. Chow *et al.* (1974) first reported the lower and additional upper dentitions of *D. similis* from the Lumeiyi Formation in the Lunan Basin of Yunnan Province, China, distinguishing *D. similis* from *D. birmanica* on the basis of several morphological differences in the lower dentitions.

The upper dentition of *D. birmanica* was discovered in Pondaung Formation during paleontological field research by Myanmar researchers in 1997 (Pondaung Fossil Expedition Team, 1997). In this study, we describe two maxillary fragments with premolars of *D. birmanica*. This discovery provides new information on the relationship of *D. birmanica* and *D. similis*.

Geological setting

The Pondaung Formation (Pondaung Sandstones) distributed in the central part of Myanmar (Figure 1) can be divided into "Lower" and "Upper" members for convenience: the "Lower Member" is mainly composed of greenish sandstone and is about 1,500 m thick in the type section; and the "Upper Member" is dominated by variegated-colored mudstone, about 500 m thick in the type section, and yields many mammalian and other vertebrate fossils (13 genera belonging to three orders; see Pilgrim and Cotter, 1916; Colbert, 1938; Holroyd and Ciochon, 1995; Jaeger *et al.*, 1999), indicative of a freshwater lagoonal environment (Colbert, 1938; Aye Ko Aung, 1999; Aung Naing Soe, 1999; Figure 2). The present material was recovered from the middle part of the "Upper Member" of the Pondaung

Formation. The Pondaung Formation grades downward into the Tabyin Formation (Tabyin Clay), and the two formations partially interfinger (Figure 2; Stamp, 1922; Bender, 1983). The Pondaung Formation is overlain by the Yaw Formation (Yaw Shale) with a distinct lithological break (Figure 2; Stamp, 1922; Bender, 1983). The Pondaung Formation is considered to date from middle to late Eocene based on the microfossil dating of the Tabyin Formation and the Yaw Formation (Bender, 1983; Figure 2). On the basis of the mammal fauna, the "Upper Member" of the Pondaung Formation has been considered most likely to be Bartonian age (late middle Eocene) (e.g. Russell and Zhai, 1987; Holroyd and Ciochon, 1994, 1995).

Systematic paleontology

Family Deperetellidae Radinsky, 1965

Genus *Deperetella* Matthew and Granger, 1925a

Diplophodon Zdansky, 1930, p. 35.

Type species.—*Deperetella cristata* Matthew and Granger, 1925a.

Other species included.—*Deperetella birmanica* (Pilgrim, 1925); *Deperetella depereti* (Zdansky, 1930) Radinsky, 1965; *Deperetella dienensis* Chow *et al.*, 1974; *Deperetella khaichinulensis* Reshetov, 1979; *Deperetella sichuanensis* (Xu *et al.*, 1979) Tong and Lei, 1983.

Distribution and age.—Asia. Middle to late Eocene.

Diagnosis.—"Deperetellids with premolar series longer than molars and posterior premolars molariform. P^{2-4} protolophs and metalophs slightly convergent to parallel, and separated lingually. P_1 and especially P_2 lengthened into shearing blades; P_{3-4} with complete hypolophs. Molars relatively shorter and wider than those of *Teleolophus*. Manus tridactyl" (Radinsky, 1965, p. 222).

Remarks.—The genus *Diplophodon* was proposed by Zdansky (1930) based on an upper dentition of *Diplophodon similis* from the Heti Formation in China. Radinsky (1965) regarded *Diplophodon* as a junior synonym of *Deperetella*, although he recognized some characteristics that distinguished *Diplophodon* from *Deperetella*. Ding *et al.* (1977), in contrast, viewed *Diplophodon* as a distinct genus, in which *Diplophodon major* Young, 1937 and *Diplophodon birmanicum* were included. We follow Radinsky's (1965) view, because it is difficult to judge based on such a scanty fossil record whether the above-mentioned differences are intra- or intergeneric variations.

Deperetella birmanica (Pilgrim, 1925)

Figures 3, 4C-D

Chasmothereium? *birmanicum* Pilgrim, 1925, p. 25, pl. 2, fig. 9.

Diplophodon similis Zdansky, 1930, p. 35, pl. 1, fig. 35; Young, 1937, p. 419, fig. 5; Zong *et al.*, 1996, p. 83, pl. 32, fig. 4; Huang, 1999, p. 129.

Diplophodon major Young, 1937, p. 421, fig. 6.

Deperetella? *birmanicum* (Pilgrim, 1925). Colbert, 1938, p. 348, fig. 40. [sic]

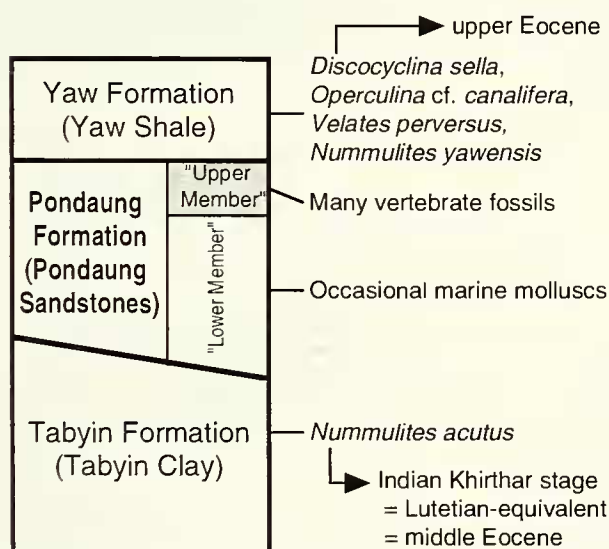


Figure 2. Generalized stratigraphy of middle to late Eocene deposits in central Myanmar and representative fossil species. Compiled from Stamp (1922), Eames (1951), Bender (1983), Holroyd and Ciochon (1994), and Aye Ko Aung (1999).

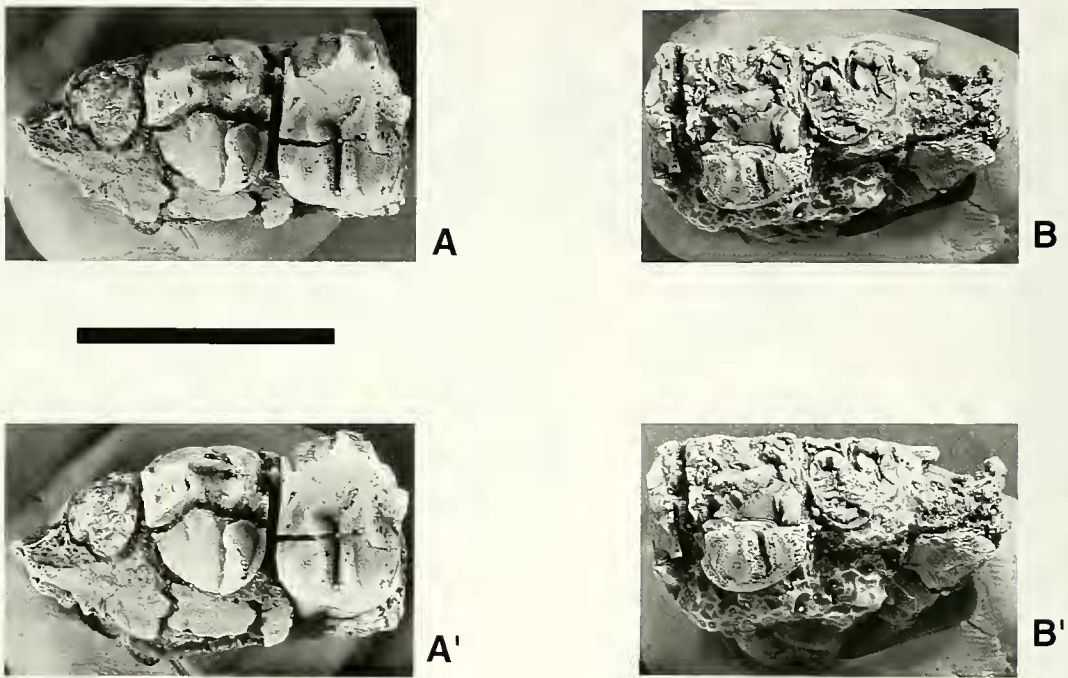


Figure 3. *Deperetella birmanica* (Pilgrim, 1925). **A, A'**. NMMP-KU 0005, stereo pair of fragmentary left upper jaw with broken P^{1-3} in occlusal view. **B, B'**. NMMP-KU 0006, stereo pair of fragmentary right upper jaw with broken P^{1-3} in occlusal view. Scale bar = 2 cm.

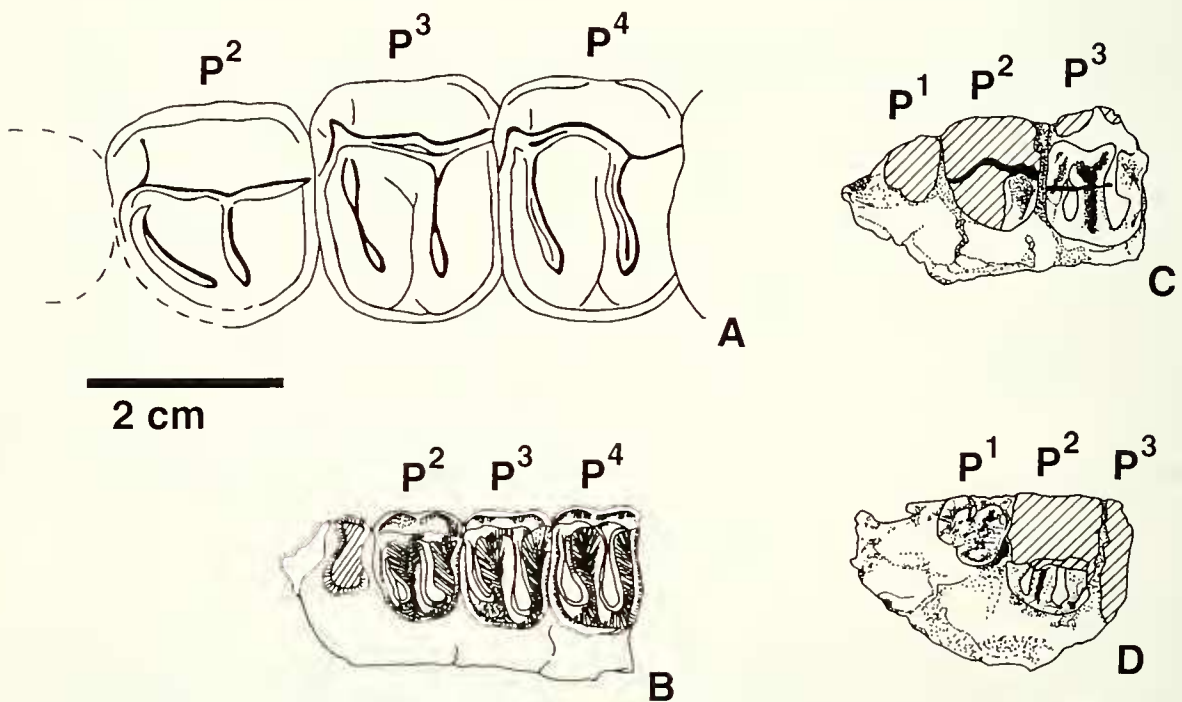


Figure 4. Upper premolar dentitions of *Deperetella cristata* Matthew and Granger, 1925a, "*Deperetella similis*" (Zdansky, 1930) and *Deperetella birmanica* (Pilgrim, 1925) in occlusal view. **A.** *D. cristata*, American Museum of Natural History (AMNH) No. 20290 with 20293, P^{2-4} , after Radinsky (1965, fig. 14). **B.** "*D. similis*" (Shanxi specimen), P^{2-4} , after Young (1937, fig. 5) and Radinsky (1965, p. 222, footnote 1). **C.** *D. birmanica*, NMMP-KU 0005, P^{1-3} . **D.** *D. birmanica*, NMMP-KU 0006, P^{1-3} (reversed). Scale bar = 2 cm.

Deperetella similis (Zdansky, 1930). Radinsky, 1965, p. 226; Chow et al., 1974, p. 263, 272, pl. 1, fig. 3, 5-7.

Deperetella birmanicum (Pilgrim, 1925). Radinsky, 1965, p. 227. [sic]

Diplophodon cf. *similis* Zdansky. Ding et al., 1977, p. 38, pl. 1, fig. 4.

Diplophodon birmanicum (Pilgrim, 1925). Ding et al., 1977, p. 44, 45.

Diplophodon qufuensis Shi, 1989, p. 91, 99, pl. 1, fig. 7.

Material.—National Museum of the Union of Myanmar No. NMMP-KU 0005, a left maxillary fragment with roots of P¹, very heavily damaged P² and relatively complete P³; NMMP-KU 0006, a right maxillary fragment with roots of P¹, lingual one-third of P² and mesial margin of P³.

Locality.—NMMP-KU 0005 was from Bahin, Myaing Township, central Myanmar; NMMP-KU 0006 was from Kyawdaw, Palé Township, central Myanmar (Figure 1).

Horizon and age.—Middle part of the "Upper Member" of the Pondaung Formation (Figure 2), middle to late Eocene (most probably late middle Eocene).

Revised diagnosis.—A small-sized *Deperetella* with half the size of the type species *D. cristata*. The dental morphology is most derived in the genus. The molar cingulum is absent or weakly developed. P² is relatively shorter and wider than that of *D. cristata*. On P²⁻⁴, the protoloph and metaloph are nearly parallel to each other, nearly perpendicular to the tooth row, and separated lingually.

Description.—P¹ has two buccolingually widened roots. The distal root is larger than the mesial one. Judging from

the roots, P¹ is longer than wide, and as long as and much narrower than P². No P¹ crown is preserved in the present material.

The crown of submolariform P² of each specimen is very poorly preserved. The protoloph and metaloph appear to be nearly parallel to each other and nearly perpendicular to the tooth row. These two are separated lingually by a groove. The distal cingula are present. There seems to be no lingual cingulum, although the tooth of each specimen is heavily worn. The existence of mesial and buccal cingula, and the characteristics of buccal structures in the tooth are uncertain.

P³ is relatively better preserved in NMMP-KU 0005 than in NMMP-KU 0006, where only the broken anterior part of the tooth is preserved. P³ is more molariform and transversely larger than P². The protoloph and metaloph are nearly parallel to each other, nearly perpendicular to the tooth row, and separated lingually by a groove. The mesial and distal cingula are present. There seems to be no lingual cingulum, although the tooth of each specimen is heavily worn. The buccal structures are not preserved. The protoloph, paracone and metaloph form a slightly oblique, inverted U-shape, and the metacone is located as buccally as the paracone.

Dental measurements and comparison with other species are given in Table 1.

Discussion

NMMP-KU 0005 and 0006 possess submolariform premo-

Table 1. Measurements (in mm) of upper premolars of NMMP-KU 0005 and 0006 and some other species of *Deperetella*. Henan and Shanxi specimens are those described by Zdansky (1930) and Young (1937), respectively. Data for "*Deperetella similis*", *D. cristata* and *D. dienensis* are from Ding et al. (1977), Radinsky (1965) and Chow et al. (1974), respectively. Abbreviations: L, anteroposterior length; W, buccolingually width; AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, China.

Specimen	P ¹ L	P ¹ W	P ² L	P ² W	P ³ L	P ³ W	P ⁴ L	P ⁴ W
<i>Deperetella birmanica</i> (Pilgrim)								
NMMP-KU 0005	7.2 ¹	6.9 ¹	9.8	12.2	9.9	14.1		
NMMP-KU 0006	7.4 ¹	7.1 ¹	9.4 ²					
" <i>Deperetella similis</i> (Zdansky, 1930)"								
Henan specimen (Zdansky, 1930)					9.0	11.5	9.4	13.4
Shanxi specimen (Young, 1937)			9.0	10.8	9.0	12.3	9.5	13.0
IVPP V29					10.0	12.8	10.7	14.3
<i>Deperetella cristata</i> Matthew & Granger								
AMNH 20290			19.9	21.8				
AMNH 20293					18.7	24.4		
<i>Deperetella dienensis</i> Chow et al.								
IVPP V31.1							13.0	20.0

¹ The measurements are based on the roots, not on the crown.

² Estimated value.

lars (P^{2-3}) which are much wider than long and have a U-shaped crista that consists of a protoloph, paracone and metaloph. The protoloph and metaloph are arranged nearly parallel and lingually separated (Figures 3 and 4C–D). These characteristics of NMMP-KU 0005 and 0006 agree well with those of the upper premolar series of *Deperetella* diagnosed by Radinsky (1965). In *Deperetella*, the lower dentitions bear a diastema anterior to P_1 (Matthew and Granger, 1925a, fig. 5; Radinsky, 1965, fig. 14). Based on this fact, the presence of a diastema anterior to P^1 in its upper dentitions can be expected, though P^1 and anterior part to P^1 have not yet been discovered in any species of the genus. The presence of a diastema anterior to the most anterior tooth or tooth roots of both NMMP-KU 0005 and 0006 strongly suggests that these tooth or tooth roots are identifiable as P^1 .

NMMP-KU 0005 and 0006 are referred to the nominal species *Deperetella similis* from China, based on the similar size and dental morphology of the protoloph and metaloph that are nearly parallel to each other and nearly perpendicular to the tooth row on P^2 (Figure 4B–D and Table 1). *Deperetella cristata* has upper premolar dentitions much larger than the present specimens, and its protoloph and metaloph on P^2 are not parallel (Figure 4A). *Deperetella khaitchinulensis* and *Deperetella depereti* are similar to *D. cristata* in dental morphology (Dashzeveg and Hooker, 1997). The dental size of *D. khaitchinulensis* and *D. depereti* is larger than that of the present specimens. *Deperetella dienensis* is also similar to *D. cristata* in terms of dental morphology (Chow *et al.*, 1974), and its dental size is intermediate between those of *D. cristata* and the present specimens. *Deperetella sichuanensis* is similar in dental size to the present specimens, but the dental morphology of the former is the most primitive among the genus (Tong and Lei, 1984).

The only deperetellid previously recorded from the Pondaung Formation is *D. birmanica*, which has so far been represented only by lower dentitions. Radinsky (1965) noticed that *D. birmanica* is more closely related to *D. similis* than to other species of *Deperetella* based on the followings; the dentitions in *D. birmanica* and *D. similis* are nearly the same size, and lack the molar cingula, which are present in *D. cristata* and *D. depereti*. He did not synonymize *D. similis* to *D. birmanica*, because *D. birmanica* was represented only by a lower dentition, while *D. similis* was represented only by upper dentitions at that time. Ding *et al.* (1977) and Dashzeveg and Hooker (1997) also recognized the dental similarity between *D. similis* and *D. birmanica*. Chow *et al.* (1974) clearly distinguished *D. similis* from *D. birmanica* because *D. similis* lacks the posterior spur on P_4 and has broadly and posteriorly convex lophids on M_{1-3} in the lower dentition. However, these differences indicated by Chow *et al.* (1974) are not useful characteristics for separating the two species, since such are probably caused only by dental abrasion: the lower dentition in *D. birmanica* (Geological Survey of India (GSI) C348) is heavily worn, while the lower dentitions in *D. similis* (IVPP V713, V31) are almost intact (see Chow *et al.*, 1974, pl. 1, figs. 3, 5–7). *Diplophodon major* Young, 1937 from the Heti Formation in China was synonymized to *Deperetella similis* by

Radinsky (1965), and *Diplophodon qufuensis* Shi, 1989 from the Huangzhuang Formation in China was synonymized to *Diplophodon similis* (= *Deperetella similis*) by Zong *et al.* (1996) and Huang (1999). Zong *et al.* (1996) and Huang (1999) did not discuss the relationship between *D. birmanica* and *D. similis*, despite the fact that the two species are very similar. Our discovery of the upper premolar dentitions of this form strongly suggests that *D. similis* and *D. birmanica* are conspecific.

Deperetella birmanica is distinguished from the other species of *Deperetella* by its smaller dental size, by the absence or weak development of molar cingula, and by the high degree of molarization in its premolar series (the lingually separated and nearly parallel protoloph and metaloph are present both on P^{3-4} and P^2) (Figure 4). This high degree of molarization in its premolar series suggests that *D. birmanica* is the most derived species among the genus *Deperetella*. Radinsky (1965), however, interpreted this fact as a result of a greater elongation of the anterior premolars in *Deperetella cristata* in contrast to the higher degree of molarization of the premolars in *Deperetella similis* (= *D. birmanica*).

The new synonymy enables us to correlate the Pondaung fauna with local middle to late Eocene mammal faunas in China, which yield *D. birmanica*, and Mongolia, which yield *D. sp. cf. D. birmanica*: Dongjun fauna of the Bose Basin, Guangxi Province, China; Lumeiyi fauna of the Lunan Basin and Xiangshan fauna of the Lijiang Basin, Yunnan Province, China; Heti fauna (from the Rencun Member) of the Yuanchu Basin, Shanxi and Henan Province, China; Huangzhuang fauna of Qufu County, Shandong Province, China; Ergilin Dzo fauna (from the Sevkhol Member) of Khoer Dzan, Mongolia (Figure 1; Li and Ting, 1983; Russell and Zhai, 1987; Shi, 1989; Zong *et al.*, 1996; Dashzeveg and Hooker, 1997; Huang, 1999). The occurrences of *D. birmanica* and *D. sp. cf. D. birmanica* suggest that these deposits are roughly contemporaneous to each other, and that these mammal faunas were mutually interchanged among them during middle to late Eocene.

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